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Grazing on green algae by the periwinkle *Littorina littorea* in the Wadden Sea

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ABSTRACT: On sedimentary tidal flats in the Wadden Sea near the Island of Sylt, the periwinkle *Littorina littorea* occurred preferentially on clusters and beds of mussels and on shell beds (100 to 350 m^{-2}), achieved moderate densities on green algal patches or mats (20 to 50 m^{-2}), and remained rare on bare sediments (<5 m^{-2}). Green algae covering >10 % of sediment surface appeared in summer on approximately one third of the tidal zone, mainly in the upper and sheltered parts and almost never on mussel and shell beds. In feeding experiments, *L. littorea* ingested more of the dominant alga, *Enteromorpha*, than of *Ulva*, irrespective of whether or not algae were fresh or decaying. The tough thalli of *Chaetomorpha* were hardly consumed. Snails feeding on *Enteromorpha* produced fecal pellets from which new growth of *Enteromorpha* started. In the absence of periwinkles, *Enteromorpha* developed on mussels and the attached fucoids. Experimentally increased snail densities on sediments prevented green algal development, but the snails were unable to graze down established algal mats. It is concluded that natural densities of *L. littorea* hardly affect the ephemeral mass development of green algae on sediments. However, where the snails occur at high densities, i.e. on mussel beds, green algal development may be prevented.

INTRODUCTION

Enhanced eutrophication appears to have led to an extensive development of green algae (Chlorophyceae) on the tidal flats of the Wadden Sea during summer (Reise, 1983; Reise & Siebert, 1994). The dominant genera are *Enteromorpha, Chaetomorpha, Cladophora* and *Ulva*. Sediments completely covered by algae turn anoxic and this affects the infauna (Soulsby et al., 1982; Hull, 1987). However, mats also provide food for herbivores and an abundant supply of detritus for deposit feeders (Price & Hylleberg, 1982; Levinton & McCartney, 1991). Ducks and geese (*Anas penelope, Branta bernicla*) are able to use algal mats as a food source (Nicholls et al., 1981). Epibenthic macrofauna like amphipods (Brenner et al., 1976; Hylleberg & Henriksen, 1980), isopods (Nicotri, 1980) and other Crustacea (Warwick et al., 1982) also ingest green algae. Nereid polychaetes anchor *Enteromorpha* and *Ulva* thalli at their tubes and ingest pieces of plant tissue (Woodin, 1977). The mudsnail *Hydrobia ulvae* occurs in high densities in the mats, but it is not known whether these snails consume green algal tissue or mainly the microflora (i.e. diatoms) covering the surface of the macroalgae (Jensen & Siegismund, 1980).

The periwinkle *Littorina littorea* is predominantly herbivorous and prefers ephemeral green algae like *Enteromorpha* and *Ulva* to all other macroalgae (Watson & Norton,

1985a). The versatility of their taenioglossan radula enables feeding on macroscopic as well as microscopic stages of algal development (Norton et al., 1990). The sporadic and patchy distribution of *Enteromorpha* and *Ulva* may render these algae too unpredictable as a food source to sustain large populations of specialist grazers (Cates & Orians, 1975; Littler & Littler, 1980). *L. littorea*, however, is a general herbivore, and efficiently uses the periodic availability of such valuable food sources (Lubchenco, 1978). Experimental exclusion of *L. littorea* on rocky shores showed that periwinkles at high densities are able to prevent the establishment of green algae (Lein, 1980; Lubchenco, 1983; Petraitis, 1983).

The influence of this herbivorous snail on the development of green algae on sedimentary tidal flats in the Wadden Sea is not known, but may be substantial – at least in habitats where snail densities are high, e.g. in beds of seagrass, shells or mussels (Wohlenberg, 1937; Linke, 1939). In this investigation, laboratory and field studies were performed to explore the importance of *Littorina littorea* for the development of green algae in different habitats in the Wadden Sea.

MATERIALS AND METHODS

Study site

Investigations were carried out in Königshafen, a shallow, sheltered Wadden Sea bay near the Island of Sylt (North Sea). Hydrography and sediments have been described by Austen (1990), distribution of macroalgae by Nienburg (1927) and Kornmann (1952). Extensive mats of green algae have been present on the tidal flats for about 10 years (Reise, 1983; Reise et al., 1989).

Distribution of periwinkles and green algae

Snail densities and the occurrence of macroscopic green algae were mapped twice, in April and July 1992, in the southern part of Königshafen. Percentage cover of green macroalgae on tidal flats was estimated visually for areas of 50 × 50 m. Meese & Tomich (1992) tested several percent cover estimation methods, i.e. visual estimation, evenly spaced dots, random dots, stratified random dots and electronic digitizing of photographic images for repeatability and robustness against observer bias. Digitizing of photographic images was found to be the most precise – but costly. The estimates derived from the other techniques were not significantly different from each other. Therefore, time-saving visual estimation was used for this investigation.

Snail densities were determined with an aluminium frame (0.25 m^2), divided into smaller areas (0.01 m^2) to facilitate counting. The frame was thrown haphazardly several metres for sampling. Seven replicate counts of snail densities were made every 50 m. Bare sediment flats, patches or mats of green algae, beds of seagrass and shells, stones, as well as clusters and banks of mussels (*Mytilus edulis*) were sampled separately with 7 replicates each, because they provide different habitats for periwinkles on tidal flats (Wohlenberg, 1937; Linke, 1939).

Ingestion rates

The ingestion of green algae by *Littorina littorea* was measured in the laboratory according to a modified method of Shacklock & Doyle (1983). Snails with a medium shell height (19 ± 1 mm, wet weight 2.15 ± 0.78 g) were sampled and placed in large Petri dishes, which were filled with sterile seawater, covered with fine meshed gauze and incubated at a constant temperature (15 °C) and photoperiod (16 h light). After a 48 h starvation period they were fed with a defined amount (wet weight) of fragmented green algae. Each experiment was run with 10 replicates over 10 days. Water and food were changed every day. The remaining algae were weighed to determine the loss due to ingestion per day. Calculations were based on wet weight of snails and algae since feeding of the snails cannot be done with dried algae. The number of fecal pellets produced was counted every morning with a binocular and examined under a microscope. Ten replicates of algae without grazers served as controls. The ingestion of *Enteromorpha, Ulva* and *Chaetomorpha* was compared. Fresh as well as decaying thalli were used to test the influence of algal condition on the ingestion rates.

Caging

Caging experiments were carried out in a sheltered part of the upper intertidal zone. Cylindrical cages made of wire-mesh (6.3 × 6.3 mm) with 54 cm diameter and 25 cm height were anchored in the sediment. For each experiment 7 cages and 7 control cages were installed, 1 to 3 m apart. *Littorina littorea* was included and excluded in different sets of experiments.

Inclusion experiments. To test the potential influence of grazing on sediment flats, densities of periwinkles were increased in a sandy area with attached strands of *Enteromorpha* covering approximately 9 % of the sediment surface. Natural density at this site was < 1 snail per m^2 in June 1992. A random choice among strands of green algae was taken to install the cages.

(a) June 4th to 20th: Each cage included 50 periwinkles corresponding to densities occurring in mussel beds (200 m^{-2}). Control cages were installed containing no snails.

(b) June 20th to July 5th: To test the effect of grazing on established algal mats, 50 snails were added to each of the control cages of (a) where the algal cover had increased.

The cover of *Enteromorpha* in the cages was estimated and photographed every day. Pictures were analysed with a screen to determine percent cover of green algae on the sediment. To estimate biomass corresponding to the algal cover in the cages, samples were taken on neighbouring sediment areas with comparable algal cover. Wet weight of *Enteromorpha* was determined.

Exclusion experiments. May 5th to August 8th: 14 cages were installed on a mud flat covered with clusters of mussels. Each cage contained a cluster with a diameter of 40 cm, which was chosen haphazardly. The periwinkles on mussels or fucoids were counted and excluded from 7 cages. Control cages contained natural snail densities. After 2.5 months, samples of mussels and fucoids were examined under a binocular microscope for the occurrence of green algal germlings.

Survival of green algae through periwinkle digestive system

Fecal pellets from *Littorina littorea* were collected and incubated in culture medium to test the ability of green algae to survive digestion. Ten snails each from two green algal mats and a sediment flat were collected and carefully rinsed in sterile seawater to remove algal remains from the shell surface. After 24 h the produced pellets were transferred to Petri dishes filled with culture medium and incubated at constant temperature (15 °C) and photoperiod (16 h light). Fecal pellets from ingestion experiments in the laboratory were treated in the same way. After 3 weeks fecal pellets were investigated for germlings of green algae.

Results were calculated as mean values with standard deviation ($x \pm y$). Data of ingestion rates were analysed by a two-factor analysis of variance (ANOVA) with algal species (3 levels) and freshness (2 levels) as factors, followed by Tukey's HSD multiple comparison test.

RESULTS

Distribution of periwinkles and green algae

The abundance of *Littorina littorea* (> 5 mm) on the tidal flats of Königshafen differed between habitats (Fig. 1). Highest densities (100 to 350 m^{-2}) occurred on hard

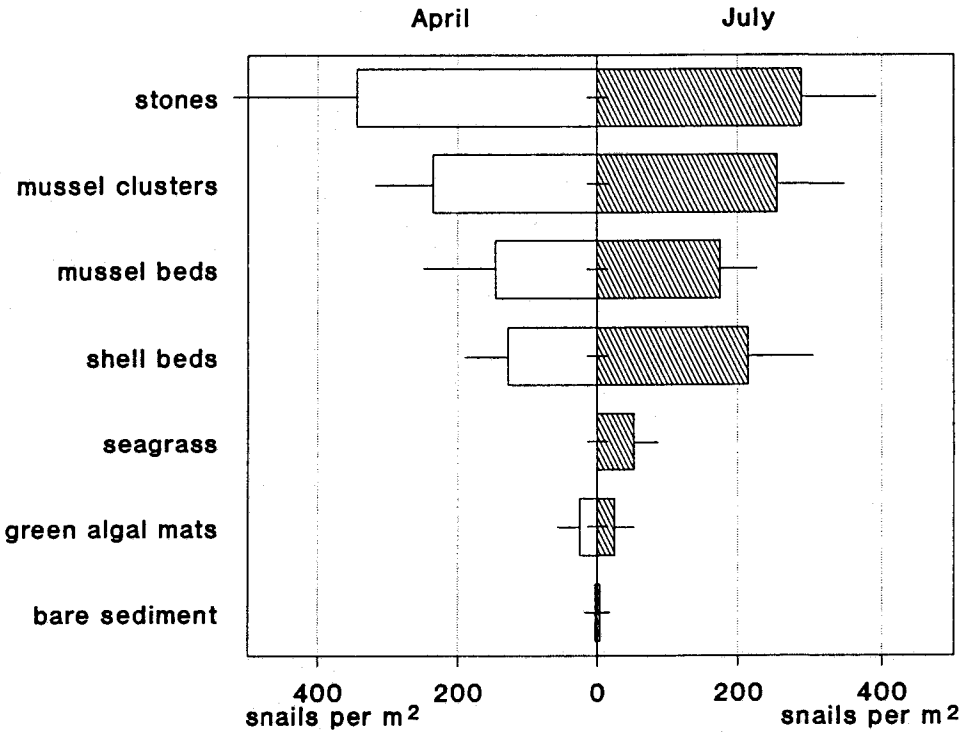

Fig. 1. Abundance of *Littorina littorea* in different habitats on the tidal flats of Königshafen (mean values and standard deviation with $n \geq 21$). Seagrass was absent in April

substrata (stones, shell beds, aggregates of mussels). Moderate densities (20 to 50 m^{-2}) were found on macrophytes (seagrass beds, green algal patches or mats). Hardly any snails were encountered on bare sediments (< 5 m^{-2}). Even on some rather small patches of *Enteromorpha* (app. 2 m^{-2}), snail densities were higher (12 to 48 m^{-2}) than on the surrounding sediments (0 to 3 m^{-2}). Green algae occurred on approximately one third of the tidal zone of Königshafen in July. Up to a 100 % cover developed in two sheltered bays, where drifting green algae accumulated. *Enteromorpha* dominated, but also large amounts of *Ulva*, *Chaetomorpha* and *Cladophora* were present. Mussel and shell beds remained free from attached green algae.

Ingestion rates

In the feeding experiments, *Littorina littorea* consumed *Enteromorpha* more than *Ulva*. *Chaetomorpha* was hardly ingested – even after a few days of starvation (Fig. 2). Data from determination of algal wet weight were analysed by a two-factor ANOVA. Significant differences among algal species were found ($p < 0.001$), but not between fresh and decaying algae ($p = 0.154$), although the latter were covered with white sulfur bacteria and had a strong smell of sulfide. Since a significant species × freshness interaction occurred ($p = 0.035$), two following one-factor ANOVA were performed, separating fresh from decaying algae. Differences between the mean of all three algal species were highly significant (Tukey's test, $p < 0.001$). Generally, the same results were obtained by determination of pellet production. Significant differences only occurred between species (two-factor ANOVA, $p < 0.001$), not between fresh and decaying algae ($p = 0.271$). The means of all three species differed significantly (Tukey's test, $p < 0.001$). Wet weight of the ungrazed controls did not change during the 24 h periods.

Inclusion experiments

Fifty littorinids per cage were able to decimate a green algal cover of 9 ± 3 % ($n = 7$) within one day to 2 ± 3 % cover. After two days, no *Enteromorpha* was left (Fig. 3). One cage was enveloped with fine-meshed gauze to capture drifting filaments of *Enteromorpha*. Since no loose thalli were encountered in the net, it is assumed that the snails ingested entire algae, and did not simply detach them from the sediment. Samples of *Enteromorpha* from areas with a comparable algal cover showed that 10 % cover of the sediment surface corresponds to 7 g algal wet weight. This was present in the cages at the beginning of the experiment. Therefore, each snail ingested approximately 110 mg *Enteromorpha* biomass daily. Ingestion rates for *Enteromorpha* measured in the laboratory were similar (127 ± 33 mg, $n = 10$). In the control cages, *Enteromorpha* strands grew rapidly. After 16 days, more than 50 % of the sediment surface was covered with green algae. At that time, 50 snails were added to the controls. These snails were not able to graze down the algal biomass. After two weeks, algal cover was still at 50 % in these cages, although snails were observed to feed on the algae just as they did in the first phase of the experiment.

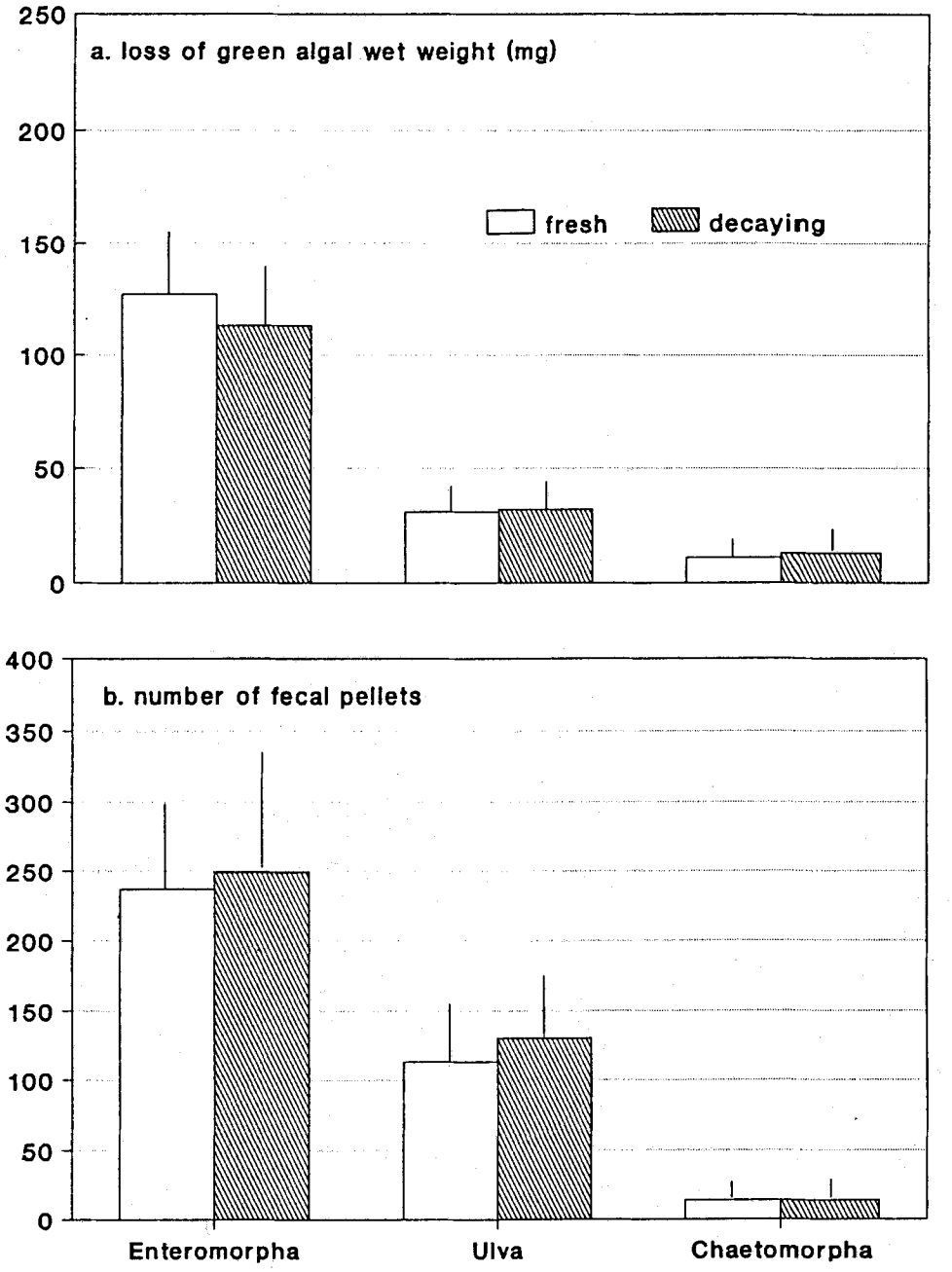

Fig. 2. Ingestion of green algae by *Littorina littorea* measured as (a) loss of green algal wet weight, and (b) number of fecal pellets produced within one day (means and standard deviation)

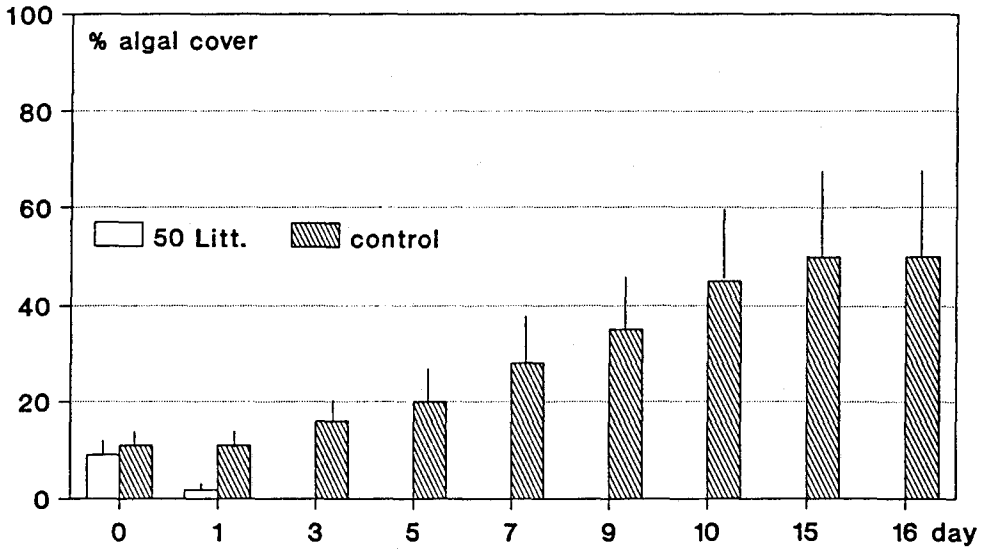

Fig. 3. Effects of *Littorina littorea* inclusion (50 snails) and exclusion (control) on *Enteromorpha* coverage within cages (n = 7 + 7) on a sandy flat over a period of 16 days

Exclusion experiments

Cages (n = 7) excluded 240 ± 32 snails from clusters of mussels. Natural densities of 244 ± 48 remained in the controls (n = 7). At the beginning of the experiment, no germlings of green algae were detected. After 2.5 months young thalli of green algae, mainly *Enteromorpha*, were attached to mussels and fucoids in the cages without periwinkles. Parts of the brown algae were covered with a dense "lawn" of green algal thalli, several mm in length. No *Enteromorpha* developed in the control cages, and none were found to develop on ambient clusters without cages.

Survival of green algae after periwinkle digestion

Fecal pellets produced in the laboratory feeding experiments contained a large amount of undigested algal tissue. Similarly, individuals collected from green algal mats produced fecal pellets with visible pieces of green algal tissue. Pellets from snails collected on bare sediment flats showed no distinct food remains. After a 3-week incubation period, germlings of *Enteromorpha* occurred in fecal pellets that were produced by snails fed with *Enteromorpa* in the laboratory experiment as well as by snails feeding in green algal mats. Pellets from snails feeding on bare sediment flats did not develop any germlings.

DISCUSSION

Distribution and abundance

Littorina littorea is able to colonize a variety of hard and soft bottom habitats (Bertness, 1984). On muddy or sandy flats, the population is highly patchy in distribution because sustained development requires a firm substrate, i. e. stones, shells or macroalgae (Bandel, 1974). These structures are of marginal or insular occurrence in the Wadden Sea tidal zone and so is the distributional pattern of *L. littorea.*

Habitat and food quality

Although *Enteromorpha* and *Ulva* are shown to be high quality food, *Littorina littorea* clearly prefers firm substrates to mats of green algae. As slow moving herbivores, periwinkles require macroalgae to serve both as food as well as habitat structure (Watson & Norton, 1985b). Green algal mats floating with the tides may provide a rather unstable habitat. Therefore, snails prefer the more stable mussel or shell beds. Here they find microscopic food like diatoms or germlings of macroalgae.

Under laboratory conditions, ingestion of different green algae was tested. *Littorina littorea* preferred the soft thalli of *Enteromorpha* and *Ulva* and hardly ingested the tough and rigid *Chaetomorpha* thalli. The toughness of the thallus surface as a barrier against grazing is an important factor for the edibility of algae (Norton & Manley, 1990). Periwinkles consumed fragmented pieces of *Enteromorpha* nearly three times more than those of *Ulva.* This is because the tissue of *Enteromorpha* is significantly softer and contains aqueous extracts with strong phagostimulant properties (Watson & Norton, 1985b). However, littorinids fed with whole algal thalli ingested *Ulva* twice as much as *Enteromorpha* (Watson & Norton, 1985a). This indicates the importance of thallus form: while the broad ulvoid thallus is easily pinned down by the snail's foot to provide a relatively stable food substratum, a single tubular frond of *Enteromorpha* is too narrow to carry the entire foot and, if inflated with gas, has a strong inherent buoyancy.

Effects of grazing

On sedimentary flats without any firm substrates (shell gravel, mussel beds), *Littorina littorea* is incapable of grazing down *Enteromorpha* because its abundance is too low. According to the literature, this was already the case prior to the advent of the green algal masses in the 1980s (Linke, 1939; Wohlenberg, 1937). Thus, the recent spread of green algae in the Wadden Sea is probably not caused by a release from grazing pressure. Furthermore, the survival of *Enteromorpha* in fecal pellets suggests that *L. littorea* would not be able to exclude these algae from the tidal zone. With increasing biomass of green macroalgae, the effects of littorinid grazing decreases because incomplete digestion is a consequence of an excess of food (Abele-Oeschger & Theede, 1991). Tissues of opportunistic green algae have a great totipotency (Santelices & Ugarte, 1987). Therefore, they are able to regenerate new thalli from undigested algal remains.

It remains an open question whether mussel and shell beds would be covered by green algal mats in the absence of *Littorina littorea.* This may be inferred from their high

abundance in these habitats and from the exclusion experiments which indicate that germlings of green algae could establish on shells, mussels and fucoids in the absence of grazing periwinkles. The effects of littorinid grazing on a shell bed was tested by means of an exclusion experiment in two aquaria, both filled with empty shells and sterile seawater. Ten snails were put in one aquarium. This is in accordance to natural densities in shell beds (250 m^{-2}). After one month of incubation in the absence of *Littorina littorea*, several mm long green algal thalli occurred on mollusc shells. No green algae were observed in the aquarium containing periwinkles.

Although grazing on microalgae has been generally presumed to be unselective, the periwinkles clearly prefer germlings of *Ulva* and *Enteromorpha* to juvenile plantlets of other algae (Watson & Norton, 1985a). However, the *Enteromorpha* thalli remained small during the 2.5 months of experimental period. Presumably there may be other inhibiting factors involved. Further experiments are required.

CONCLUSIONS

Although *Enteromorpha* is a preferred food of *Littorina littorea*, effects of grazing on sedimentary flats are small compared to those documented from rocky shores. The underlying cause is the unsuitability of *Enteromorpha* as a habitat when growing on sediments. In the Wadden Sea tidal zone, *L. littorea* is not, and probably never was, a grazer controlling green algal growth. A possible exception is the lack of green algae on most mussel beds.

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